ART. VI. A PROBLEMATICAL CAT-LIKE MANDIBLE FROM THE UINTA EOCENE, *APATÆLURUS KAYI*, SCOTT

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(Plate VII)

Apatælurus kayi Scott, Science, N.S., Vol. 85, May 7, 1937, p. 455.

Director Avinoff of the Carnegie Museum, Pittsburgh, very kindly sent me for description a remarkable fossil, collected by Mr. J. Leroy Kay, of the Carnegie Museum staff, from the Middle Uinta beds (Section B) of northeastern Utah, in the summer of 1936. At first, I took for granted that this jaw belonged to an unmistakable sabre-tooth, specialized in an astonishing degree for an Eocene genus, and prepared a description of it on that hypothesis. In the course of the study, however, doubts regarding the correctness of this reference began to arise, doubts which were shared by my colleague, Professor G. L. Jepsen, who suggested that both rami of the mandible be photographed with X-rays, a procedure by which important information was obtained.

The drawings accompanying this article were made by Sydney Prentice of the Carnegie Museum.

The specimen consists of the two separate halves of a lower jaw, the left half containing two of the cheek teeth and the right four. The dental formula is not altogether certain, but appears to be: $i?_2$, c_1, p_4, m_2; incisors and canines are all missing and represented only by the alveoli, the number of which is not quite free from doubt, but, according to appearances, there were two, possibly three, close-set and laterally compressed incisors and a much larger canine, also narrow and compressed, but far smaller than the lower fang of an ordinary carnivore, whether creodont, or fissiped. That the upper canines were laniary sabres is indicated by the protective flanges on the lower jaw, and this inference is corroborated by the evident reduction of the lower canine.

The number of premolars would seem to be different in the two rami; on the left side all the premolars have been lost, and alveoles for only

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three are preserved. Of these, the foremost one is small, for a single-rooted tooth, and is separated by a short gap from the next succeeding one. This is, presumably, the socket of p_1, while that for p_2, which must have been lost during the lifetime of the animal, was filled up by a secondary deposit of bone. The alveoli of p_3 and p_4 are double-rooted and the latter are much the larger, though the two for p_3 are larger than the minute tooth in the right ramus would lead one to expect. The molars, m_1 and $_2$, are in place and almost exactly like those of the right side.

In the right half of the mandible four teeth are preserved, molars $_1$ and $_2$ and premolars $_3$ and $_4$; in addition, the alveoli of p_1 and $_2$ are visible, the former single-, the latter double-rooted. The foremost premolar (p_3) is minute, but is implanted by two roots, nevertheless. The crown has the compressed conical shape characteristic of the predaceous dentition, but retains a number of vestigial features, which indicate that it has undergone reduction from a more complicated type of tooth; the apex of the cone is bifid and two ridges enclose a posterior valley; there is a conspicuous posterior basal cusp and a very small anterior one, an enamel tubercle rather than a cusp. The last premolar (p_4) is a greatly enlarged copy of the third; it is triconodont, with three cusps in the same antero-posterior line, the middle one of which is very much the largest, and the anterior basal cusp is far larger than in p_3; a fairly deep valley, on the inner side, is enclosed between the principal and posterior cusps. The three cusps are decidedly convex on the outer side and both of these premolars, p_3 and $_4$, have a backward inclination like the last premolar of *Eusmilus* and both are almost completely unworn, though a very slight degree of abrasion is observable on p_4. The contrast between p_4 and m_1 in regard to wear is very conspicuous.

The first molar (m_1) is decidedly smaller than p_4 and very much smaller than m_2. A suspicion that this might perhaps be a milk-tooth was refuted by the X-ray negative, which clearly showed the stout roots of the tooth and demonstrated the absence of any tooth-germ in the jaw. The lower end of the posterior root is seen in the photograph to be recurved, a difference from all of the other teeth. The crown is much abraded, but all its elements are still distinct and it is decidedly like the same tooth in *Hyænodon*, it is a small carnassial, worn on the outer side by the shearing of the anterior upper sectorial, p^4; the blade is made up of two compressed, sharp-edged, trenchant

cusps, of which the posterior one has a bifid apex. This division persists in spite of the extensive wear which the tooth has suffered, for the abrasion is confined to the buccal, or external, side of the crown; in addition to the shearing blade, there is a relatively large heel, which is a single-pointed cusp.

The second molar, m_2, is much the largest of the cheek-teeth and anteriorly is overlapped by the heel of m_1. The shape and general aspect of this tooth are very feline, but not more so than in such creodonts as *Hyænodon* and *Patriofelis*. The crown is a shearing blade, made up of two cusps and much worn on the outer side, but so abraded as to keep the cutting edge sharp. The posterior cusp shows a vestige of the bifid apex, which is so distinct in m_1; a very faintly marked groove being the unmistakable remnant of this division. The talon also is reduced to vestigial proportions, but is very distinct.

So far as the cheek-teeth are concerned, there is nothing surprising or unusual about this jaw; these teeth differ no more than generically from those of *Patriofelis* or *Oxyæna*, but the mandible itself is little short of astonishing. My first impression, as noted above, was that the fossil must be referable to the machairodont subfamily of the Felidæ, and I was greatly surprised to find so highly specialized a sabre-tooth in the upper Eocene, for the resemblance of this mandible is not so much to *Hoplophoneus* as to *Eusmilus*, much the most advanced and specialized of all the Oligocene machairodonts, whether in the Old World or the New. One notable difference between the sabre-tooths and the true cats is in the length of the jaws, which in the former are not nearly so abbreviated as in the latter; and this, in turn, is associated with the different manner of using the jaws and canine teeth. A true feline *bites* and holds its prey with firmly closed jaws, for which action the reduced leverage of the short jaw is favourable. A sabre-tooth could not bite, for the great upper tusks barred entrance to the mouth.

The hypothesis of Matthew and Merriam, now so widely accepted, has been all but demonstrated by the remarkable *Nimravus* skull from the upper White River beds, now in the museum of the State School of Mines, Rapid City, So. Dak. This skull, which was described and figured by Scott and Jepsen,[1] shows a terrible wound through the left frontal bone, which, according to surgical opinion, must have been inflicted at least a month before the victim's death. The shape and

[1]Trans. Amer. Philos. Soc. N.S. Vol. XXVIII, p. 148, Pl. XXI.

size of the wound make it highly probable that it was caused by a stabbing blow from the tusk of *Eusmilus*, the large sabre-tooth contemporary of *Nimravus*. The position of the glenoid cavity and mandibular condyle made it possible for the machairodonts to drop the lower jaw so far as to free the points of the upper canines. As the late Professor W. D. Matthew suggested, the sabre-tooth cats must have used their sabres as a venomous snake uses his fangs, striking a stabbing blow with the whole head. The mechanism of the jaws and areas of muscular attachment combine to support the Matthew-Merriam hypothesis, and the nature of the wound mentioned above makes it well-nigh certain. As will be seen, an understanding of the jaw-mechanism in the sabre-tooth cats is essential to the interpretation of *Apatœlurus*, which displays so extraordinary a resemblance to the machairodonts, though belonging to a very different and but distantly related suborder of the Carnivora.

The mandible of *Apatœlurus* is deceptively like that of *Eusmilus* and is astonishingly far advanced in specialization for an Eocene mammal. The anterior face of the horizontal ramus is squarely transverse and forms a right angle with the buccal side of the jaw, the demarcation between the two surfaces making a conspicuous ridge, which is almost as prominent as in *Eusmilus*. The anterior surface, or mental area, differs from that of the latter in several details; it is, so far as preserved, plane vertically, not made concave by the prominent projection of the incisive alveolar process. The mental foramen and groove seen in the White River genus are absent. The symphysis is prolonged vertically so far as the bone remains, and is relatively more extended antero-posteriorly than in the latter. The flange, which served as a protection for the sabre, is, unfortunately, broken away on both sides, so that its shape and size are indeterminable. It was, however, unmistakably present, and it may be inferred from the intact portions of the borders, that it was not so largely developed as in *Eusmilus*, and its external, or buccal, surface was not so deeply concave. The dentary portion of the ramus is relatively shallower and more slender than in *Eusmilus*.

The ascending ramus, while very similar, in general, to that of *Eusmilus*, differs in a number of details. The masseteric fossa is much more deeply impressed and has more definite borders. The coronoid process has a stronger backward inclination and is even more reduced in height; though, as the process has suffered some loss in

both rami, it is not feasible to estimate the exact difference. The condyle has an even more inferior position than in *Eusmilus*, farther below the level of the teeth, but, in shape, it is very much as in that genus; its position is nearly horizontal, and most of its transverse length is external to the plane of the coronoid; the dorso-ventral diameter of the condyle diminishes rapidly to the outer side, the ventral border being steeply inclined. In *Eusmilus* and *Hoplophoneus* the condyle has a similar shape. As in those genera, the angular process is short and projects very little behind the condyle, the emargination above which is much deeper than in the White River machairodonts, setting off the condyle more distinctly. The angle has a decided inflection, so much so as to suggest marsupial affinities, but the teeth forbid any such reference. A broad channel runs forward from beneath the condyle to the inferior dental foramen, which is placed much nearer to the ventral border than in the Oligocene cats, and the channel is more clearly marked than in them.

MEASUREMENTS	mm.
Inferior dental series, length i_1 to m_2, incl.	102
Canine alveolus, ant.-post. diameter	10
Canine alveolus, transverse diameter	5
Lower cheek-teeth series, length	59
Lower premolar series, length	34
Lower molar series, length	30
Lower third premolar, ant.-post. diameter	5
Lower third premolar, transverse diameter	3
Lower fourth premolar, ant.-post. diameter	12
Lower fourth premolar, transverse diameter	6
Lower first molar, ant.-post. diameter	12
Lower first molar, transverse diameter	5
Lower second molar, ant.-post. diameter	Right 20 Left 19
Lower second molar, transverse diameter	8 7

The measurements of the lower jaw are made in comparison with those of *Eusmilus dakotensis* (Princeton Univ. Mus. No. 11,079).

	Eusm. mm.	*Apat.* mm.
Mandible, extreme length from condyle	175	149
Mandible, depth of horiz. ramus below m_1	32	27
Mandible, thickness of horiz. ramus below m_1	15	13
Mandible, breadth of ramus at chin	20	13
Mandible, condyle, transverse width	30	25
Mandible, condyle, height above ventral border	31	18
Mandible, ventral width of angle	12	12

For this remarkable fossil the name *Pseudælurus* would be very appropriate, were not that term preoccupied by a genus of felines. It is proposed, therefore, to name the genus *Apatælurus* (from ἀπάτη, deceit) which expresses the same idea; the species *kayi*, which is defined by the measurements, is named in honour of Mr. J. L. Kay, of the Carnegie Museum, who discovered the type and only known specimen.

The form of the mandible, with its characteristic flanges, demonstrates, beyond peradventure, that in this animal the upper canines were laniary sabres, and the position of the mandibular condyle shows that the jaws could be opened as widely as in any of the machairodonts. No doubt these "sham sabre-tooths," as they may be called, used their tusks in delivering a stabbing blow such as the machairodonts almost certainly did. Cope has already used "false sabre-tooths" for *Nimravus* and its allies, otherwise that term might well be applied to these Eocene imitators of the true machairodonts.

Systematic Position of Apatælurus

Though it seems incredible that this astonishing fossil does not represent a sabre-tooth cat, yet such is the inevitable conclusion from the facts above detailed. Not only is this animal not a machairodont, it is not even one of the fissiped carnivores. The highly specialized sectorial, which is so very feline in character and appearance, is not the first lower molar (m_1) as it is in all of the Fissipedia, but the second (m_2) as in those of the Creodonta which possess shearing carnassials. To the Creodonta, therefore, this genus must be referred, but the family to which it belongs is not so obviously indicated. The relatively very small first molar is an important point of resemblance to the Hyænodontidæ, to which it is quite possible that *Apatælurus* should be referred. All things considered, however, it seems more likely that this genus is one of the Oxyænidæ, which are so much more numerous and diversified in the North American Eocene. Lacking the upper teeth and skull, no definite choice between these alternatives can be made, but to one or other of these families the Uinta fossil almost certainly belongs.

The principal oxyænid of the Bridger (middle Eocene) is *Patriofelis*, and it may be that *Apatælurus* represents the sabre-tooth branch of the same stock. The "*Ælurotherium*" of Adams suggests itself as

a near ally of the Uinta genus, but it would not be possible to regard this Bridger animal as ancestral to the Uinta *Apatælurus*. The obscurity which has veiled *Ælurotherium* has lately been cleared away by Mr. Robert H. Denison, a graduate student in Columbia University, who is making an intensive examination of the Oxyænidæ. He writes me: "The Princeton specimen (No. 11,875) which was originally described by Wortman as ?*Patriofelis leidyanus*, and later removed to a new genus, *Ælurotherium*, by Adams, was considered by both authors to consist of p_3 to m_1. However, Matthew's contention that these teeth were milk molars of *Patriofelis ferox* is completely substantiated by a specimen of the latter species in the U. S. National Museum (No. 13,818) containing d_c and m_1 erupting, and three milk molars which correspond very closely in size and other respects with the three teeth of the type of *Ælurotherium leidyanum*."

Another Bridger genus which is of interest in this connection is the *Machairoides* of Matthew, in which he reported that the small flanges of the mandible indicate that the upper canines were, at least, beginning to take on the sabre-like form.

General Considerations

For more than half a century, palæontologists have been familiar with the conceptions of parallel and convergent evolution. Cope, in particular, insisted upon the reality and frequency of these processes, which may be briefly defined as the independent acquisition of similar characters in unrelated groups. Zoölogists, as a class, long resisted any admission of the possibility of such independently repeated acquisitions, though nowadays the reality of convergence as a normal mode of evolution is very generally accepted. Indeed, it is in danger of being overworked. Admitting that convergence has not infrequently taken place, the question immediately arises as to how far it can be carried. It is not yet possible to fix limits to the process, other than to say that identity is very rarely, if ever, attained.

In the case of *Apatælurus* we have two alternative explanations of its paradoxical features: Either (1) it is a real machairodont, or (2) it is a creodont which has imitated sabre-tooth characteristics. That the second alternative is the less unlikely one, is the writer's conviction. On the first hypothesis, it will be necessary to assume that the creodont family, oxyænid, or hyænodontid, developed a highly

specialized type of dentition, reducing the first lower molar (m_1) and converting the second (m_2) into a cat-like sectorial and then, reversing the process, transforming the reduced first molar into an enlarged sectorial and diminishing the large second molar to a useless vestige. While we are not in a position to declare that such a mode of development is impossible, it can be said that no instance of such a reversal is known.

On the other hand, equally astonishing cases of convergence have been well-nigh demonstrated. The marsupial sabre-tooth *Thylacosmilus*, discovered by Mr. E. S. Riggs in the Catamarcan Pliocene of Argentina, is a most surprising imitation of *Eusmilus*, not only in the great, sabre-like upper tusk and in the form of the mandible with its immense protective flanges, but also in all of the mechanism for opening the mouth so widely as to clear the points of the sabres and delivering a stabbing blow with the head. That this mechanism should have been independently developed a third time, is unexpected, but there is no ground for maintaining that it could not have happened.

EXPLANATION OF PLATE VII

Apatælurus kayi, Scott
Carnegie Museum, No. 11920
(All figures, three-fourths natural size)

FIG. 1. Outer view of right ramus.
FIG. 2. Occlusal view of right ramus.
FIG. 3. Inner view of right ramus.
FIG. 4. Outer view of left ramus.